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THE RELATION OF ANIMAL NUMBERS TO CLIMATE.

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The object of the present paper is to describe in outline some of the recent developments of that branch of animal ecology which concerns the numbers of wild animals, and to point out certain directions in which co-operation between the meteorologist and the biologist would be advantageous to both. There is undoubtedly an encouraging tendency for meteorologists to attempt as far as possible to adapt their methods to the needs of workers in other branches of science, botanists and zoologists in particular. At the same time there is often a definite lack of desire to co-operate, which is partly due to the natural and fatal inertia which seems to imprison the different departments of science in their own private channels of research, as soon as they become at all specialised ; but is also due to a genuine ignorance of the existence of those borderline problems in which co-operation would be fruitful. It is with some of these borderline problems that this paper is concerned.

I hope to be able to show also that meteorologists and climatologists, whilst always providing the main part of the basic data upon which the biologist is dependent for the success of his work, can also obtain from animals useful clues to the existence of climatic phenomena which might otherwise pass unnoticed. In other words the idea of using animals as *indicators* of climatic behaviour can be more widely exploited than it is at present.

The prevailing opinion among meteorologists appears to be that this idea (as exemplified in the subject of " Phenology ") has been tried out on a large scale, and has failed to throw upon climatic behaviour any light which would not have been shed more fully by the study of thermometers, barometers, sunshine-recorders and rain-gauges. With this opinion one cannot help agreeing, in so far as the methods hitherto employed are concerned : in most cases the results appear not merely to throw no light upon meteorology, but to throw no light upon anything, in spite of the undoubted pleasure and training in observation which the work involved gives to the people who make the records. It is quite possible to make a huge series of observations on some particular thing (e.g. the index

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numbers of motor cars) and to construct from the data maps which show certain regular features of distribution ; but it does not follow that the maps are of the slightest use to anyone.

Let us take the example of the dates of arrival of migrating birds in the British Isles. If these dates are determined by climatic factors (which is not certain), they are determined by the climates of the countries from which the birds start to migrate, or through which they pass on their way to the British Isles. And since an observer in, say, Yorkshire has no means of knowing exactly what country the birds do come from, or what countries they have passed through on the way, his observations on the dates of their arrival in Yorkshire must be practically valueless climatologically or meteorologically. The dates of birds' songs, the first appearance of bumble-bees (of which there are half a dozen common species, with different habits and ecology), and similar records, are equally of doubtful value. In face of such fragmentary and complex data, the meteorologist may well exclaim, as Œdipus did to the priest, " Nor had I any help from birds."

When we come to consider the relation of the *numbers* of animals to climate, the position is different. In order that the problem may be clearly appreciated, it is necessary first of all to say a little about animal numbers in general. Recent ecological research has established the fact that animal populations seldom remain constant in numbers from one year to the next, or even from one month to the next. In some cases the fluctuation in numbers is very great, in others it may be less conspicuous. Again, some animals may remain almost constant for a year or two, and then show some sudden and violent increase or decrease. In fact, both the period and the amplitude vary in the different animals to an enormous extent ; at the same time the variation may either be quite irregular, or else it may have an astounding regularity. The Cockchafer (*Melolontha vulgaris*) is subject to marked cycles in its numbers, and appears usually every three or four years in large numbers. The details of this periodicity vary in different parts of Europe, but in any one place it may be extraordinarily constant. In certain parts of Europe the Cockchafer outbursts (" Flugjahr ") have occurred exactly every three years for the last sixty years (Decoppet, 1920)(²). It appears probable that practically no species of animal is able to keep its population absolutely constant. This certainly applies to most mammals (e.g. moles, mice, rabbits, squirrels, wild deer and sheep, and even hippopotami and elephants) ; most birds (e.g. game-birds such as grouse and partridges, and many small birds such as tits and thrushes) ; all fishes that have been studied, and marine fish in particular ; most insects (e.g. cockchafers, locusts, butterflies, wasps, mosquitoes, etc.) ; and a very large number of other animals.

The question which concerns us here is the extent to which climate is concerned in causing these fluctuations. Now, there is not sufficient information available to enable us to make any general statement

on this point. We should however expect that these variations in the population would tend to come into close relationship with the fluctuations in climate which are of such universal occurrence all over the world. As concrete illustrations of this relationship, I shall take certain species of mammals, in which the phenomena are clear-cut, long series of records available and in which we know something at least of the purely biological factors which are at work. (The insects are being treated elsewhere by another author.*)

Lemmings and Mice.—In all countries of the world in which the subject has been investigated, wild mice and voles are subject to very violent and sometimes astonishing fluctuations in numbers. In the northern and alpine regions of the northern hemisphere the mice and voles are largely replaced by various species of lemmings. These, too, undergo striking fluctuations in their numbers, sometimes culminating in the spectacular migrations about which so much has been written. It has been possible to obtain a long series of records of the lemming migrations of Norway (which are caused by periodic over-population in their mountain homes in the south or on the tundra of the north). These records show that the onset of migration has usually occurred quite regularly every three or four years, and they thus form an accurate index of the periodic increase of the lemming numbers in their natural habitats. Thus there were lemming years in 1918, 1922, and 1926.

The records collected by Collett ([3]) also prove that not only the lemming, but all species of Norwegian voles and mice (including the Wood-Lemming), are subject to the same periodicity, whether they live in the alpine regions of the mountain, in the woods, or in the lowlands. Furthermore, there is a similar cycle in numbers of the rype or willow grouse in Norway, and a comparison with the lemming cycle shows that in the past the two cycles ran practically parallel for a number of years (Kloster, 1921) ([1]). In Norway, therefore, there is a periodic waxing and waning among a number of wild animals belonging to different species.

It can be shown that although disease attacks the mice and lemmings when they reach a peak in numbers, so that the epidemic might conceivably be the widely acting cause that brings all the different species into line, the rype suffers from epidemics caused by entirely different organisms from those which attack rodents. Furthermore, the hypothesis of universal epidemics does not explain how such widely separated areas as the Dovre, Trondhjem region, and Tromso Valley, may be undergoing a simultaneous inundation of lemmings or mice. There is evidently in action some cycle of climate which acts upon all these animals. There is a strong indication, on various grounds, that this cycle may be one of snowfall, which does vary in a very marked manner in Scandinavia. It is, however, very difficult to obtain data about the amount of snow

* See paper by B. P. Uvarov.

actually lying on the ground (which is the condition that affects animals), as distinct from the total amount precipitated.

Turning now to England, we find a similar four (sometimes three) year cycle in mice, affecting all the mice in England and Scotland in the same years. 1922 and 1926 were mouse years in Britain. There is a strong suggestion of a correlation between the English mouse years and the Norwegian lemmings and mouse years, but this has not yet been conclusively proved. In any case, we have to postulate some factor acting widely over the British Isles.

Similar periodicities have been worked out for the mouse-plagues of Central and Western Europe, and when these are placed by the side of the extraordinary and well-attested periodicity of the cockchafer (*Melolontha*) in Europe, little doubt is left in one's mind that there are important periodic weather factors at work which have not yet been properly elucidated.

If we turn now to North America, we find that the lemming and mouse cycle is also important and well marked in that country. The records of arctic fox skins caught by the Hudson's Bay Company in Ungava Bay (Northern Labrador) during the last eighty years form a fairly good index of the periodic cycle of the lemming in that region, since lemmings form the main food of the fox. When these records are analysed, it is seen that the cycle is very regular, and also that there is an extremely high correlation between the years of lemming maxima in Ungava Bay and of lemming maxima in Norway ([4]). It is not possible here to present any details of the evidence bearing upon this whole problem. Briefly, it can be shown that, roughly speaking, all the region covered by the low-pressure area centred over Iceland (i.e., Northern Labrador, Baffin Land, the north-west point of Hudson's Bay, Scandinavia as far east as Finmark, the British Isles, and probably Greenland) have mouse or lemming cycles which tend to come in the same years. The correlation is considerably higher than that which would be expected on chance. It appears, therefore, that some climatic cycle acts on this low-pressure area as a whole, possibly affecting rainfall or snowfall.

It may also be mentioned that the ptarmigan in Labrador has a cycle in numbers, similar to that of the Norwegian willow-grouse, and also correlated with the lemming cycle.

Varying Hare in Canada.—The remarkable periodic cycles in numbers of the varying hare or snowshoe rabbit in Canada have long been known, especially through their influence upon the fur-trade of Canada ; for the snowshoe rabbit is the food of the fox and the lynx, and other fur-bearing animals ; and when the rabbits disappear the fur-bearers starve or leave the district.

The snowshoe rabbit has a cycle in numbers of ten years (which has been going on for at least 90 years, as shown by direct evidence, and for over 120 years as shown by the indirect evidence derived from statistics of lynx skins). The source of evidence for these statements

is the Hudson's Bay Company, who have always been interested in the problem, and of recent years have, on the initiative of the present governor, Mr. C. V. Sale, been carrying out active investigations into these periodicities and their causes.

A similar ten-year cycle in the numbers of other animals has also been observed. This is true of such fur-bearing mammals as the wolf, the mink, the fisher (a large weasel), and the pine marten (the Canadian equivalent of the Russian sable). Particularly good statistics are available for the fisher, and these show that its cycle has run parallel to that of the varying hare, but in an opposite sense. Thus, while rabbits were at a peak in the east of Canada in 1904 and 1905, the fishers were at their peak several years earlier, 1898 and 1899. This general relationship has been preserved for the last sixty years at least.

It can also be shown that the muskrat's numbers are dependent directly upon the water levels of the lakes, swamps and streams in which it lives, and that there is a fluctuation in these levels which probably controls the muskrat numbers.

In regard to the rabbits, the control of their cycle by climate is proved by the fact that not only do their numbers vary, but also the *rate of reproduction* (number of young in a litter and number of broods in a season). Such a variation in rate of reproduction could only be produced by changes in outer conditions. Here then, we find a ten-year cycle in animal life, obviously bound up with climate, and operating over an area of many million square miles. This cycle shows the same curious regularity as the mouse cycle, in so far as it acts simultaneously over wide areas. Roughly, it covers most of the northern coniferous forest belt of Canada, an area from which long period rainfall statistics are unfortunately almost lacking.

Discussion.—I have taken two examples of mammal fluctuations in order to illustrate the fact that climate plays a very important part in the mechanism, although it is not, of course, the only important factor. The elucidation of these cycles happens to be of great importance economically, as well as from a scientific point of view. For instance, the mouse cycle is one of the worst problems of forestry, since voles eat or destroy seedlings of trees, and even young trees themselves. In Labrador, the mouse-cycle affects almost every living thing, and is one of the keys to the native life. In Europe, mouse-plagues are frequent and costly, and so far little controlled. The rabbit-lynx-fox cycle affects the fur-trade, and rabbits are an important factor in destruction of planted seedlings of forest trees. In South Africa, and in the Volga region in Russia, the rodent cycle is the key to the problem of plague, for every few years there are outbreaks of endemic plague caused by the periodic epidemics of wild rodents.

It will thus be seen that the study of wild animal numbers is beginning to become an important branch of animal ecology, and

one which requires the help of meteorologists. But the brief and condensed accounts given above of two particular cycles in animal life should make it clear that the meteorologist has also something to gain from studying these cycles. The occurrence of animal cycles over large areas, and repeated in a regular way over long periods of years, seems worthy of attention. The present situation is that ecologists are finding processes at work for which they are compelled to postulate climatic variations of a certain type ; but, at the same time, are unable to gather much assistance from the meteorological statistics.

Is the search for climatic cycles controlling certain phases of animal life a wild goose-chase ? Is it a pure accident that lemmings have the same years of abundance in Ungava Bay and Norway, or that sandgrouse irrupt in huge numbers from central Asia every twenty-two years, or that grouse and snowshoe rabbits in Canada, otherwise unconnected ecologically, have parallel ten-year cycles, though not in the same years ? Or is there something still lacking in the methods by which meteorological statistics are collected which makes them unsuitable for the use of biologists, who are studying organisms that integrate a number of different external factors into the one process—reproduction ?

Organizations.—It may be of interest to mention in conclusion the chief organizations which are at present attempting to collect and co-ordinate the data necessary for forming proper conclusions about the cycles in numbers of different animals. As will be seen, they are all concerned directly or indirectly with animals of economic importance. The situation at present is similar to that which would exist in meteorology, if meteorologists were unable to study their subject as a pure science, and were forbidden to send up kite balloons or organize expeditions to the antarctic regions. The result is that the organizations dealing with animal numbers are rather in the form of isolated efforts.

Plague.—There are a number of plague research stations in different countries, and owing to the importance of rodents as reservoirs of plague, some of these stations have begun to make systematic records of the fluctuations in numbers of these animals in their own districts. The most important work that is being done in this connection is in South Africa, by the Department of Public Health and the Johannesburg Institute for Medical Research. Other stations that might be mentioned are those at Saratov (in the Volga Region of the U.S.S.R.) ; and at Harbin in Mongolia, where the marmot cycle is under observation.

The Fur Trade.—The Hudson's Bay Company is carrying out extensive research into the Canadian mammals, with particular reference to the fur trade, but has adopted a very broad-minded policy in regard to the scope of the work.

British Work.—The work of co-ordinating the cycles in numbers of British (and to some extent, European) mammals, such as mice, squirrels and rabbits, is being carried on at the Department of Zoology and Comparative Anatomy in Oxford University, partly with the help of the Empire Marketing Board. The main research work on cycles for the Hudson's Bay Company is also centred here.

Mouse Plagues on the Continent.—The Biologische Reichsanstalt für Land und Forstwirtschaft in Berlin, the Department of Agriculture of Bavaria, and the Hauptstelle für Pflanzenschutz at Landsberg-Warthe, and various other German centres of agriculture, publish annual maps of great value, showing the state of the mouse population in Germany for each year. Similar work is done in some other countries, but is not so well centralised.

Game Birds.—The existence of important fluctuations in the numbers of certain game-birds has stimulated various bodies of sportsmen to start enquiries into the causes of the periodic scarcity which affects their sport. Among these might be mentioned the British enquiry into grouse disease in Scotland, which did not, however, have more than a temporary existence. The most active permanent investigations are those carried out by the Norwegian Grouse Committee, which is chiefly concerned with the willow grouse ; and by the Massachusetts Fish and Game Association in New England, upon cyclical increase and decrease of the ruffed grouse.

Fisheries.—It is impossible to do more than mention the existence of work upon fluctuations in the numbers of fish, which have an important correlation with oceanographical factors, and therefore indirectly with the climate.

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